

A NEW SPECIES OF *QUINKANA* MOLNAR (EUSUCHIA:
CROCODYLIDAE) FROM THE MIOCENE CAMFIELD BEDS
OF NORTHERN AUSTRALIA.

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ABSTRACT

Quinkana timara sp. nov., from the Miocene Camfield Beds of northern Australia, is a Eusuchian crocodylid with serrated, laterally-compressed teeth. In common with species of *Pristichampsus* (Gervais) from Europe and North America, the new form has a ziphodont dentition, deep narrow rostrum, laterally-directed orbits, and a straight, dorsal profile of the rostrum in lateral view. The other species of the genus, *Quinkana fortirostrum* Molnar, is unusual in having a relatively broad snout. It is not yet possible to establish whether features shared by *Pristichampsus* species and *Q. timara* sp. nov. are convergently evolved, or are an indication of some close relationship.

KEYWORDS: *Quinkana timara* new species, Eusuchia, Crocodylia, ziphodont, Miocene, Camfield Beds, Australia.

INTRODUCTION

Amongst crocodylians, the *Sebecosuchia* (Simpson), *Hsisosuchidae* Young and Chow and the Eusuchian *Pristichampsinae* Kuhn are remarkable for having serrated, laterally-compressed teeth. Langston (1973: 291) introduced the vernacular term 'ziphodont' (Greek: sword-toothed) to describe the condition of the teeth as an alternative to the more cumbersome descriptive 'dinosaur-toothed'. Most crocodylians have conical, unserrated teeth.

The South American *Sebecus icaeorhinus* Simpson, 1937, and North American and European species of *Pristichampsus* (Gervais) are amongst the most complete, and best known ziphodont crocodylians (e.g. Colbert 1946; Langston 1956, 1975; Kuhn 1938; and Berg 1966). The synonymy of *pristichampsines* is reviewed or discussed by Berg (1966), Langston (1956, 1975) and Steel (1973). Here I follow the summary of Steel (1973). In addition to their unusual teeth, these two genera evolved convergently a distinctive morphological complex that is widely accepted as being indicative, at least in part, of a terrestrial mode of life. In his synthesis of the Crocodylia, Steel (1973: 50) lists

those features of the *Sebecus* cranium that may have suited it to life on land, though a contrasting interpretation was published by Langston (1965: 135) who suggested, by analogy with *Paleosuchus* Gray (see also Steel 1973:86), that *Sebecus* "may also have frequented high energy water courses". Kuhn (1938:324) discusses features of *P. rollinatti* (Gray) (= *Weigeltisuchus geiseltalensis* Kuhn 1938) that suggest a terrestrial habitus.

Whatever their habits in life, *Sebecus* and *Pristichampsus* species are generally considered to represent a convergently-evolved crocodylian ecomorph (e.g. Buffetaut 1989: 33, Langston 1973) having deep, narrow snouts, laterally-facing orbits and similar quadrate morphology (Langston 1973: fig.4). In *Sebecus*, the external nares also open laterally, while *P. rollinatti* has hoof-like ungual phalanges, and a probably round rather than laterally-compressed tail (Kuhn 1938). Viewed laterally, *pristichampsines* have a relatively flat dorsal snout surface. However, in *Sebecus* it is arched, both conditions contrasting with the dorsally-concave profile typical of essentially aquatic crocodylians.

The fundamental difference between the Eusuchian *pristichampsines* and the

Sebecosuchia, however, lies with the position of the internal nares (choanae), rather than with any differences in their adaptive complexes for supposed life on land. In Sebecosuchians, the internal nares are large and relatively more anterior in position, bounded by both the palatines

and pterygoids, while in Eusuchians they are proportionally smaller and occupy a posterior position entirely within the pterygoids.

The presence of ziphodont crocodylians in Australia was reported by Hecht and Archer (1977), who identified two types of laterally-

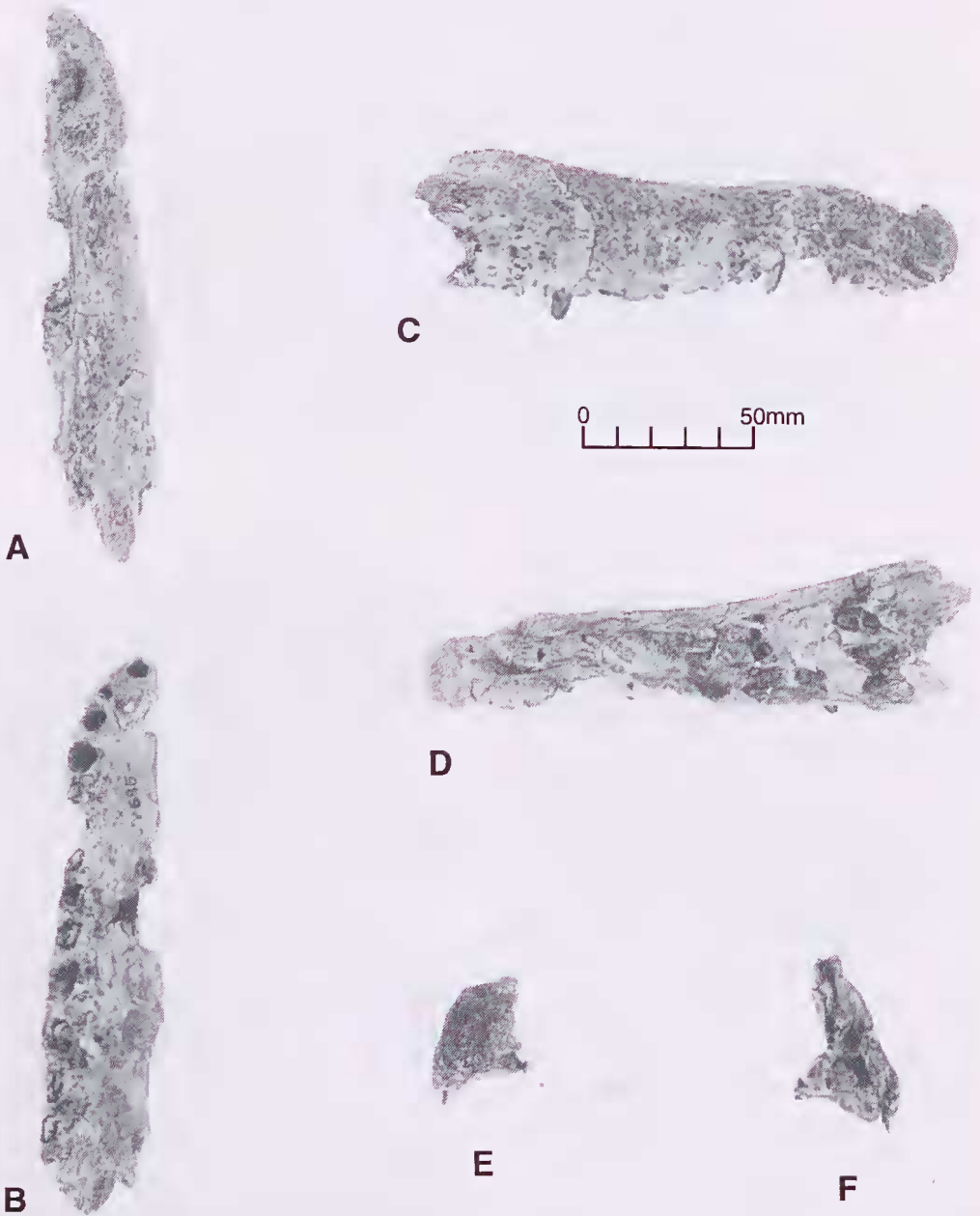


Fig. 1. Partial *Quinkana timara* sp. nov. holotype, NTM P895-19, composed of the right maxilla and premaxilla, in: A, dorsal; B, ventral; C, lateral; D, medial; E, anterior; and F, posterior views. In the line drawings, sutural surfaces are shown in stippie and in the medial view the narial passage is hatchured. Abbreviations: a.w.fpt, anterior wall of the pterygoid fossa; e.n., external nares; fsp, palatal fenestra; i.f., incisive foramen; ims, intermaxillary suture; ips, interpremaxillary suture; l.c., lateral maxillary chamber;

compressed teeth from Quaternary sediments, and described two maxillary fragments representing two distinct species. They suggested that both the *Sebecosuchia* and *Pristichampsinae* might be represented in the Australian fossil record. Earlier in the same year, Molnar (1977)

provided an initial description of an almost complete, though edentulous, snout of an apparently ziphodont crocodilian of Pleistocene age from Tea Tree Cave, Queensland, which was eventually designated the holotype of *Quinkana fortirostrum* Molnar, 1981. Molnar (1981) con-

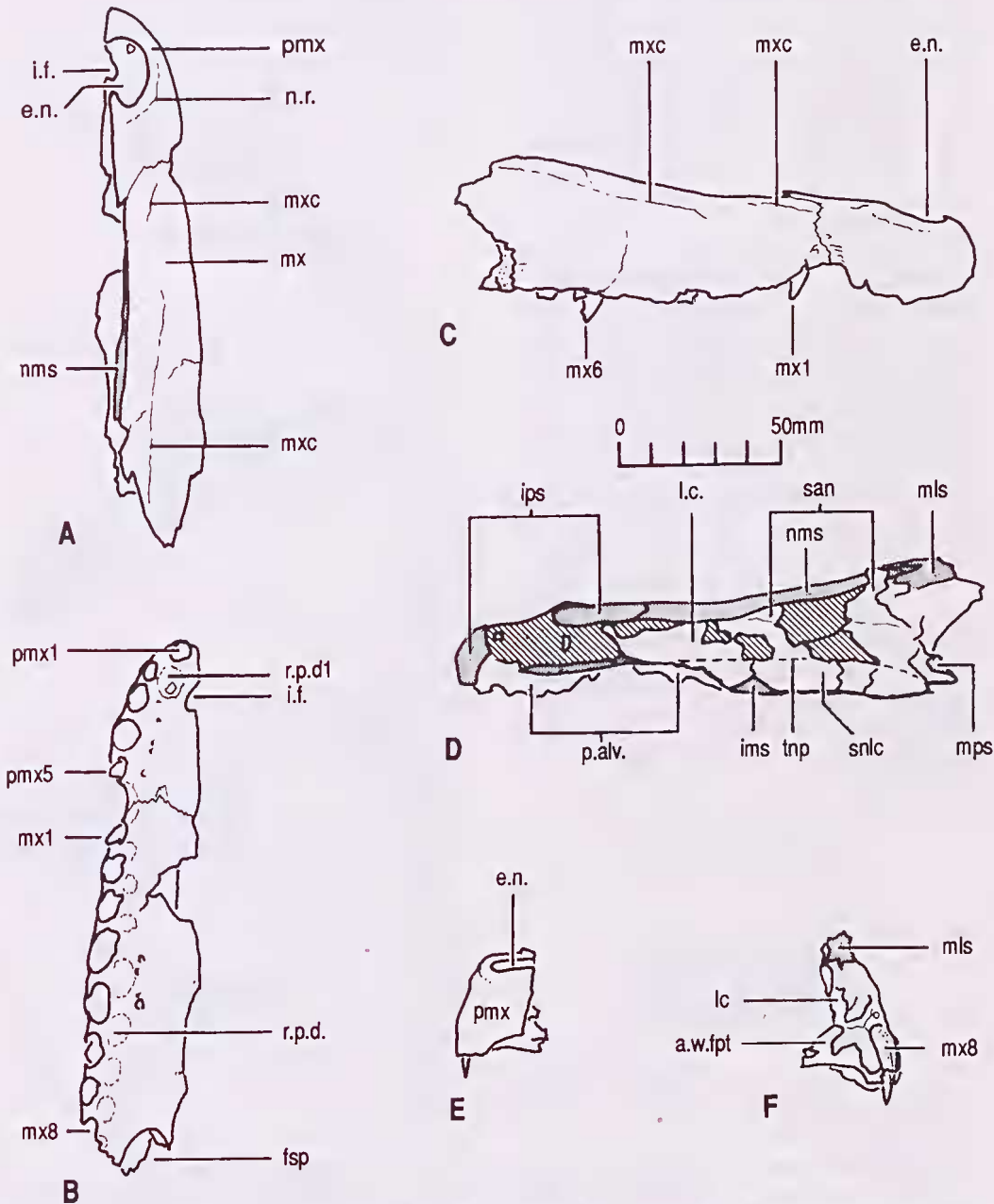


Fig. 1 (cont.):mps, maxillopalatine suture; mx, maxilla; mxc, maxillary crest; mx1-mx8, maxillary tooth or its alveolus, numbered from the anterior end; nms, nasomaxillary suture; n.r., narial rim; p.alv., alveolar processes of the maxillary and premaxillary dentition; pmx, premaxilla; pmx1-pmx5, premaxillary tooth or its alveolus, numbered from the anterior end; r.p.d, reception pit for dentary tooth; r.p.d1, reception pit for first dentary tooth; san, supra-alveolar niche of the lateral chamber; snlc, sub-narial portion of the lateral chamber; tnp, trace of the ventral floor of the narial passage.

cluded that *Q. fortirostrum* was possibly also a terrestrial crocodile, though differing from other ziphodonts in having a relatively broad snout.

The new Bullock Creek species is placed in *Quinkana* because it shares with *Quinkana fortirostrum* a distinctive ziphodont dentition, and a pattern of antorbital excrescences on the dorsal surface of the rostrum that appears to be unique to this genus. In snout proportions, the new ziphodont from Bullock Creek is more similar to species of *Pristichampsus* than it is to *Quinkana fortirostrum*, but whether these and other similarities are convergently evolved or indicative of close relationship cannot yet be resolved.

Detailed comparisons between the known Australian fossil crocodylians are outside the scope of this paper. However, such studies will be required to develop comprehensive differential diagnoses, and to more satisfactorily resolve the systematics of Australian fossil Eusuchians. Four extinct crocodylian genera are currently recognised from Australia. The extinct Australian forms are species of *Quinkana*, *Pallimnarchus pollens* de Vis; *Harpacochochampsia camfieldensis* Megirian, Murray and Willis 1991; *Baru darrowi* Willis, Murray and Megirian 1990; and *Australosuchus clarkae* Willis and Molnar 1991.

Institutional prefixes to catalogue numbers are abbreviated as follows: AM, Australian Museum, Sydney; FMNH, Field Museum of Natural History, Chicago; Me, Hessisches Landesmuseum Darmstadt, Germany; NTM, Northern Territory Museum, Darwin; QM, Queensland Museum, Brisbane; UCMP, University of California Museum of Paleontology.

SYSTEMATICS

Eusuchia Huxley
Crocodylia Gmelin
Crocodylidae Cuvier
Quinkana Molnar, 1981

Type species and type locality. *Quinkana fortirostrum* Molnar, 1981; holotype AM F57844; Tea Tree Cave, Queensland.

Revised generic definition (after Molnar 1981:809). Eusuchian crocodylid with the following combination of characters: rostrum proportionally deep; anterior margins of palatal fenestrae coincident with the anterior walls of the pterygoid fossae; two distinctive eminences

present on lacrimal and one on prefrontal, anterior and dorsal to the orbit margin; antorbital shelf above the nasolacrimal foramen, adjacent to base of prefrontal eminence; jugal proportionally deep; shallow sub-orbital jugal sulcus (inferred for *Q. fortirostrum*) confluent with lateral concavity of the posterior maxilla; palatal portion of maxillary-premaxillary suture broadly U-shaped with convexity directed posteriorly; palatal bulges coincide with sub-narial extensions of the 'lateral chambers' of the maxillae; maxillary alveoli elongate with long axes typically inclined to the lateral snout margin; narial aperture wider than long.

Quinkana timara sp. nov.
(Figs 1-5, 8-9)

Type material examined. From the Bullock Creek Locality, Camfield Station, Northern Territory (Latitude 17° 7'S, Longitude 131° 31'E): HOLOTYPE - from the 'Blast Site', NTMP895-19, two fragments, one composed of the right premaxilla and maxilla, maxilla incomplete posteriorly, and the other composed of the left lacrimal, prefrontal and partial jugal. The two fragments were collected in the same mass of limestone, and on the basis of juxtaposition, preservation and relative sizes are thought to represent one individual. Extracted using acetic acid. PARATYPES - from the 'Blast Site', NTM P895-16, edentulous left dentary fragment retaining four complete and two incomplete alveoli; NTMP894-6, anterior part of a left dentary with eight alveoli and one tooth *in situ*: from an unrecorded Bullock Creek Locality quarry, NTM P8691-3, left posterior maxillary fragment from alongside the palatal fenestra, retaining three serrated, laterally-compressed teeth and partial alveoli for two other teeth.

Referred specimens. From 'Dromornithid Mountain' (Bullock Creek Locality), NTM P8697-2, jugal: from the 'Blast Site', NTM P87115-13 and NTM P87108-24, isolated ziphodont crowns: from unrecorded Bullock Creek Locality sites, NTM P862-24, NTMP862-23 and NTM P87105-43, isolated ziphodont crowns.

Comparative material. *Quinkana fortirostrum* holotype, AM F57844, Tea Tree Cave, Queensland; *Baru darrowi*, holotype NTM P8695-8, and referred specimens NTMP87105-6, NTM P87103-8, all from the 'Blast Site', Bullock Creek Locality; neontological *Crocodylus porosus*, NTMP926, Darwin Croco-

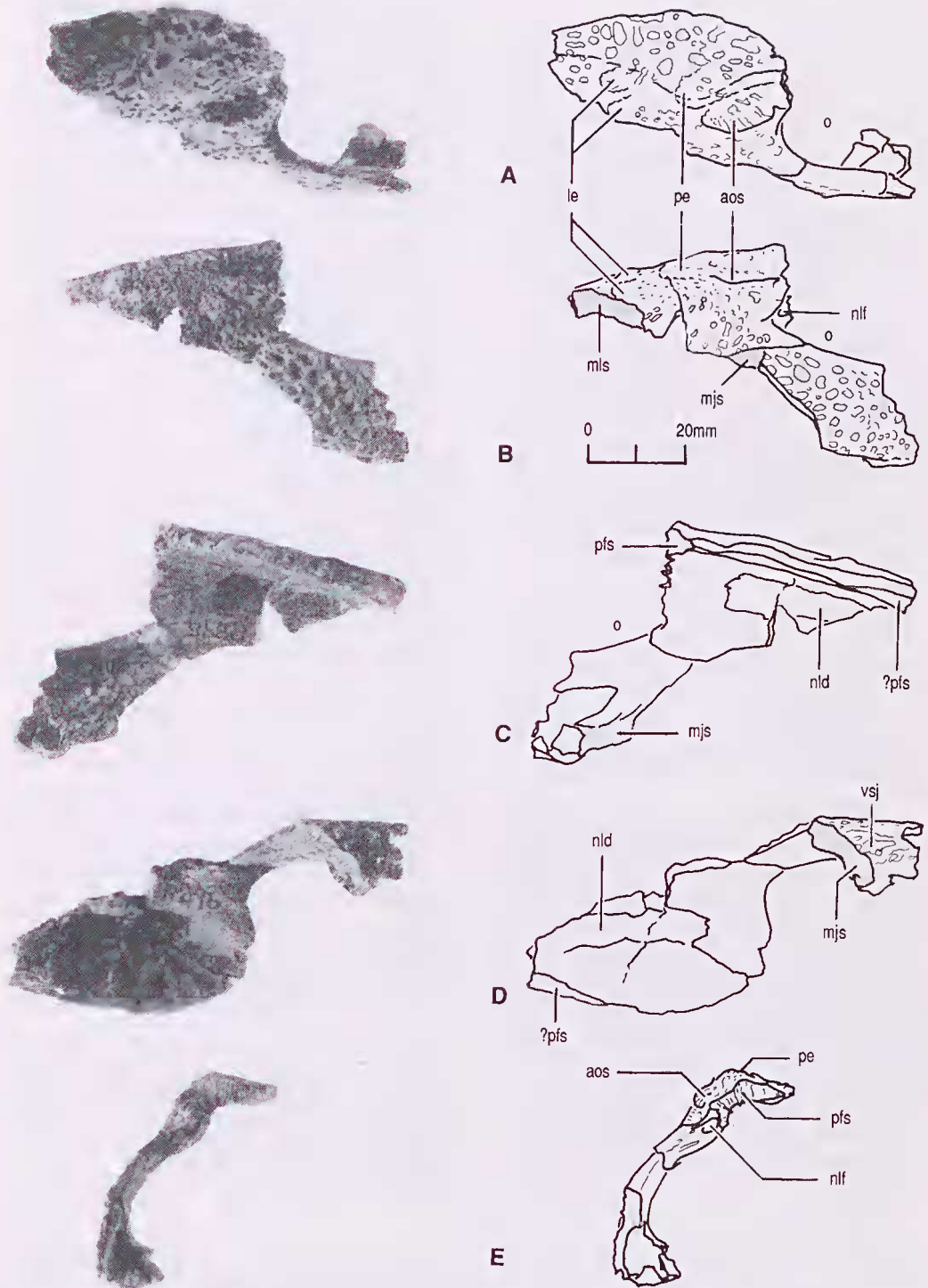


Fig. 2. Partial *Quinkana timara* sp. nov. holotype, NTM P895-19, composed of the left lacrimal, prefrontal and partial jugal in: A, dorsal; B, lateral; C, medial; D, ventral; and E, posterior views. Sutural surfaces are shown in stipple. Abbreviations: aos, ante-orbital shelf; le, lacrimales; mjs, maxillo-jugal suture; mls, maxillo-lacrimal suture; nlf, nasolacrimal foramen; nld, naso-lacrimal duct; o, orbit; pe, prefrontal excrecence; pfs, prefrontal-frontal suture; vsj, ventral sculptured area of the jugal.

dile Farm, 40km, Stuart Highway.

Age. The *Quinkana timara* sp. nov. material described here is part of the Bullock Creek Local Fauna from the Camfield Beds. The age of the fauna is estimated from the relative stage-of-evolution of marsupial components of the Bullock Creek Local Fauna, according to methods outlined in Woodburne *et al.* (1985). The Bullock Creek Local Fauna is considered younger than the Kutjamarpu Local Fauna (Wipajiri Formation) of South Australia, older than the Alcoota Local Fauna (Waite Formation) of central Australia, and mid to late Miocene in age (Woodburne *et al.* 1985, Rich 1991).

Diagnosis. Differs from the other known species, *Q. fortirostrum*, in having a narrower snout, proportionally larger antorbital shelf, slightly greater degree of festooning, and on the basis of alveolar morphology, probably more size-differentiation in the teeth. In ventral view, the maxillo-jugal suture is transversely broad, lying anterior to a triangular sculptured area. Ventrolateral margin of the dentary ramus developed into a low crest.

Description. The *Quinkana timara* holotype, composed of an entire premaxilla and virtually complete maxilla from the left hand side (Fig. 1), and a fragment composed of right lacrimal, prefrontal and partial jugal (Fig. 2), has been restored to show the shape of the complete rostrum (Figs 3, 4), with snout proportions given in Table 1.

In restored dorsal aspect, the external narial aperture of *Q. timara* is large, and positioned close to the anterior margin of the premaxillae. The widest dimension of the narial aperture lies towards the front of the opening. In dorsal view, the aperture has a bi-lobed appearance: posteriorly, the nasals, which probably projected a short distance into the aperture, were buttressed laterally by a short anterior projection of the premaxillae, while anteriorly the premaxillae have a short, delicate posterior projection at the mid-line. An internarial septum is absent. In lateral view, the external narial aperture is deeply notched, indicating that the nostrils opened somewhat laterally.

The holotype premaxilla was breached dorsally, within the narial vestibule, by the tip of the first dentary tooth. The narial aperture is bounded posteriorly by a distinct, but very low and gently-rounded, rim. The incisive foramen is relatively small and rounded-triangular to cardioid in out-

line, with the apex pointing anteriorly.

Notable features of the *Q. timara* maxilla, in dorsal view, include the absence of lateral undulations (lateral festooning of Langston 1975:295), presence of a pre-orbital crest (continued from the lacrimal as described below), presence of a very weakly defined crest over the first maxillary tooth, and a notch ('crocodylid notch') for the fourth dentary tooth at the maxillo-premaxillary suture. The preorbital crest defines the transition in the posterior half of the rostrum from the planar dorsal surface to the steeply inclined, slightly convex, lateral maxillary face (Figs 1F, 3B). The maxillary convexity is probably confluent with a sub-orbital jugal sulcus (described below).

While no nasals have been found yet for *Q. timara*, their structure may be deduced from a restoration (Fig. 3B). Their combined outline is parallel-sided where bounded by the maxillae, tapering anteriorly between the premaxillae to contribute to the posterior margin of the narial aperture, and tapering posteriorly between lacrimals and prefrontals. In the absence of a frontal bone, the position of the naso-frontal contact is uncertain.

The *Q. timara* holotype had five premaxillary teeth, as evidenced by the alveoli, but the total number of maxillary teeth cannot be precisely determined. The maxilla retains eight complete or partial alveoli, while maxillary alveoli eight to 12 are interpreted to be present on the paratype NTM P8691-3 (Fig. 5). Most alveoli are laterally compressed, though the degree of compression varies somewhat along the tooth row (Fig. 1B) being generally more pronounced in the posterior teeth. One complete and five broken teeth are retained in the holotype (NTM P895-19) while three complete examples are present in the paratype (NTM P8691-3). The first maxillary

Table 1. Snout proportions of *Quinkana timara* sp. nov. compared to selected ziphodonts (after Molnar 1981: Table 1). H = height of the rostrum at the fifth maxillary tooth, W = the width of the rostrum at the fifth maxillary tooth, and L = the length of rostrum measured between the anterior orbit margin and the posterior margin of the narial aperture.

Taxon	H/L	H/W index of snout depth	W/L index of snout width
<i>Sebecus icaeorhinus</i>	0.39	1.37	0.28
<i>Pristichampsus vorax</i>	0.24	0.51	0.48
<i>Quinkana timara</i>	0.26	0.61	0.41
<i>Quinkana fortirostrum</i>	0.36	0.51	0.70

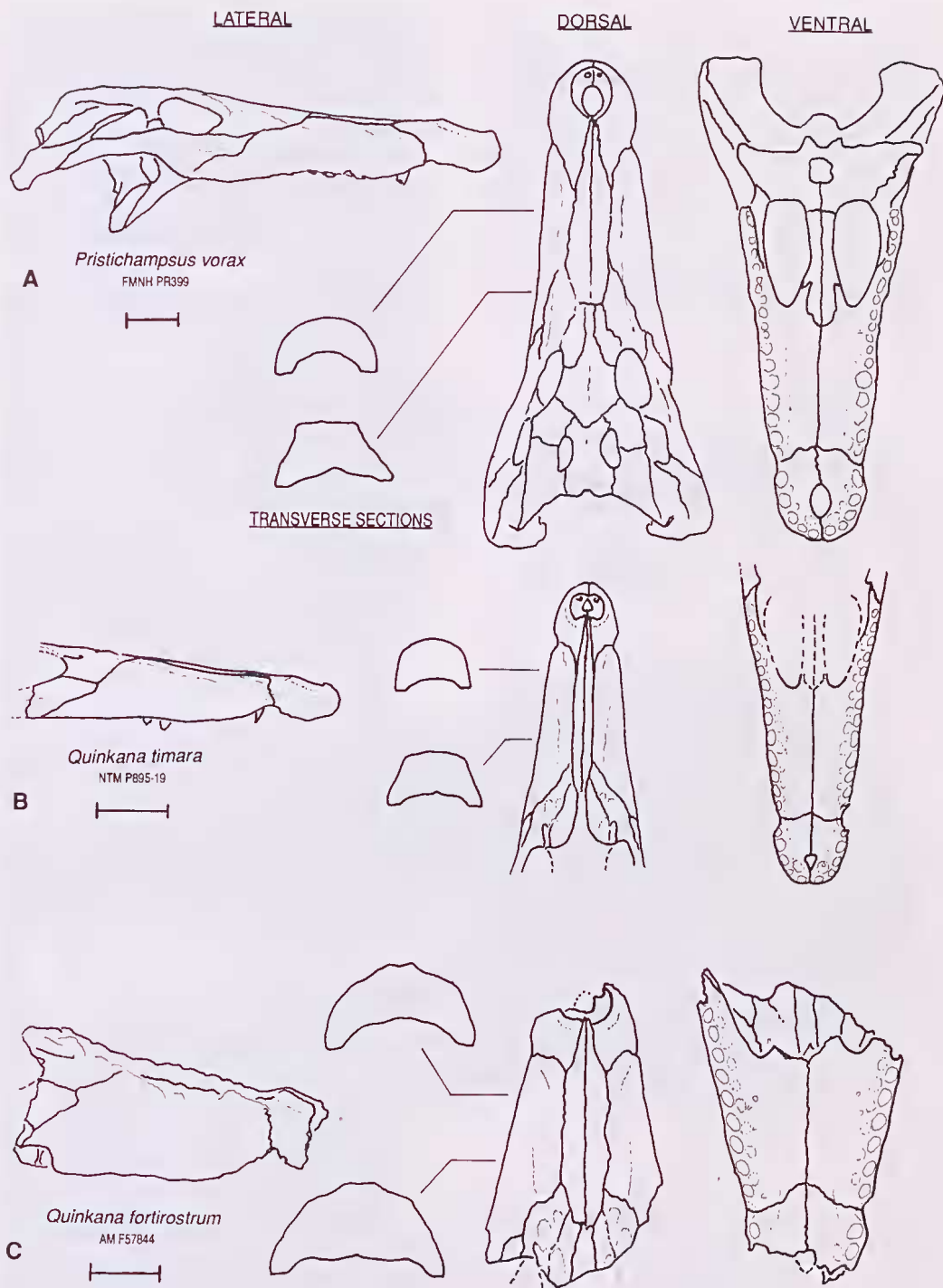


Fig. 3. Comparison of the skull shape of: A, *Pristichampsus vorax* (after Langston 1975: figs 1 and 2); B, a restoration of *Quinkana timara* sp. nov., based on the best fit of the two NTM P895-19 fragments and P8691-3; jugal P8697-2 was not incorporated because it comes from a larger individual and is too robust (probably an ontogenetic allometric effect) to match the P895-19 individual; and C, *Q. fortirostrum* holotype AM F57844; the lateral view is a reversal of the more complete left hand side. Some of the sutures in *Q. timara* sp. nov. are uncertain, and are based on *Q. fortirostrum*. Scale bars are all 50mm. The three skulls are scaled so that the distance between the anterior orbit margin and the posterior margin of the external nares is constant.

tooth of the Bullock Creek holotype has a distinct posterior curvature in lateral view, such that the leading edge of the tooth is longer than the trailing edge, while the more posterior teeth were evidently proportionally shorter (dorsoventral dimension) and longer (anterior-posterior dimension) (Table 2). A selection of isolated teeth showing these characteristics from the Bullock Creek Local Fauna are portrayed in Figure 6. In all Bullock Creek examples, the carinae are very finely and evenly serrated, averaging seven to ten serrations per millimetre. The dentary teeth oc-

cupied reception (occlusal) pits lying medial and intermediate to the maxillary teeth when the jaws were closed, in an 'overbite' configuration.

It is apparent from the alveoli of *Q. timara*, and in some cases from the *in situ* teeth, that the long (anteroposterior dimension) axes of the teeth were generally inclined to the lateral snout margins (Figs 1B, 5A). The alveoli lie within an alveolar process projecting ventrally below the level of the palate, which thus appears vaulted in cross-section (Fig. 3). Palatal morphology is distinctive. Anteriorly, from the incisive foramen,

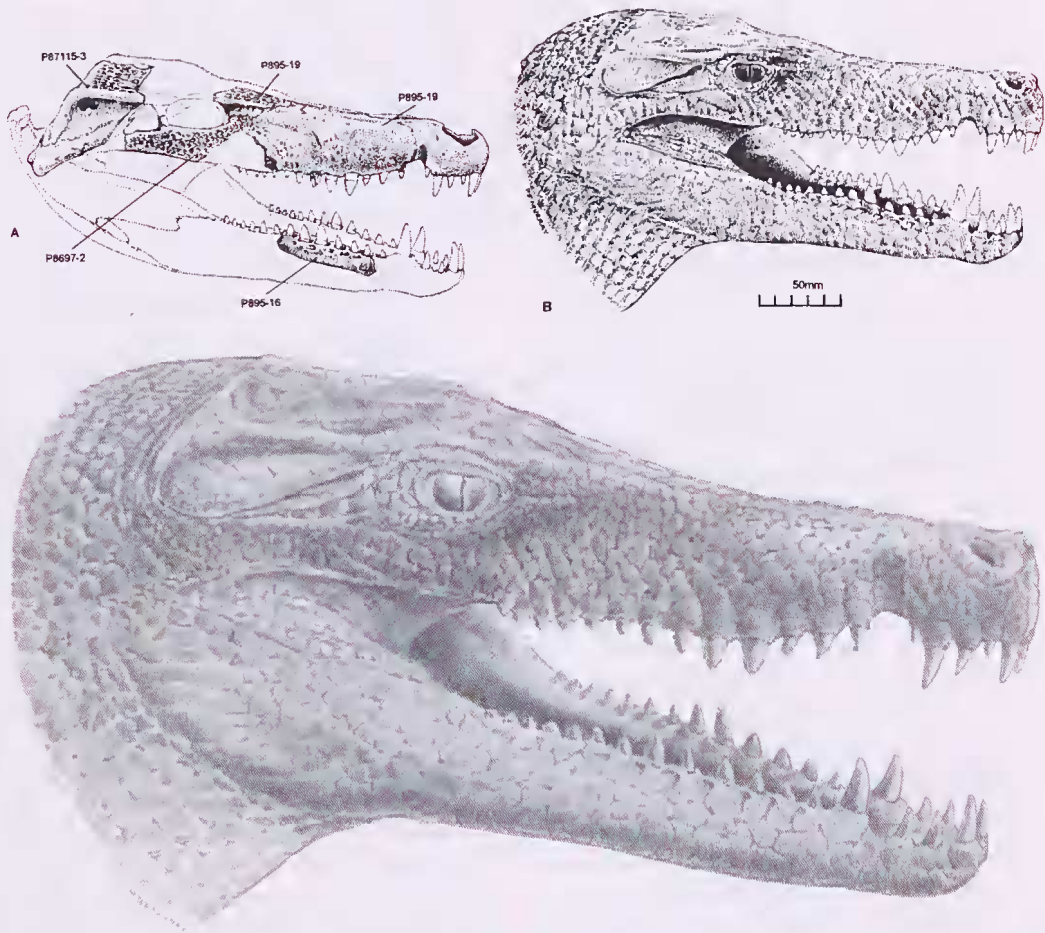


Fig. 4. Reconstruction of *Quinkana timara* sp. nov. based on: A, holotype fragments P895-19, paratype P895-16 (dentary), referred specimens P8697-2 (jugal), and an unassigned skull deck (P87115-3) of an individual with features and proportions suggesting a relationship to *Quinkana*. The reconstruction was completed before the paratype NTM P895-38 (symphyseal part of a dentary) was available for study. There are no definite contacts between the individual specimens. P8697-2 has been scaled down to match the orbital margin represented on P895-19. Because of its much larger size, the vertical dimension of the sub-orbital portion of P8697-2 is probably deeper relative to its length than it should be, and consequently the orbit would have been somewhat larger than shown; B, significant features of the reconstruction are the laterally-directed nostrils, indicated by the deeply notched profile of the external narial aperture, the laterally-directed eyes with a distinct antorbital crest, and the deep, slab-sided and transversely-narrow snout. The occipital region and occipital condyle of the possible *Quinkana* skull deck are more ventrally directed than in *Crocodylus*, suggesting a head-erect posture, in contrast to the more typical crocodylid head-horizontal posture. Because a young individual is depicted, the jaw festoons are shown minimally developed. The number of posterior teeth depicted is conjectural, based entirely upon the space available for their presence in the overall reconstruction.

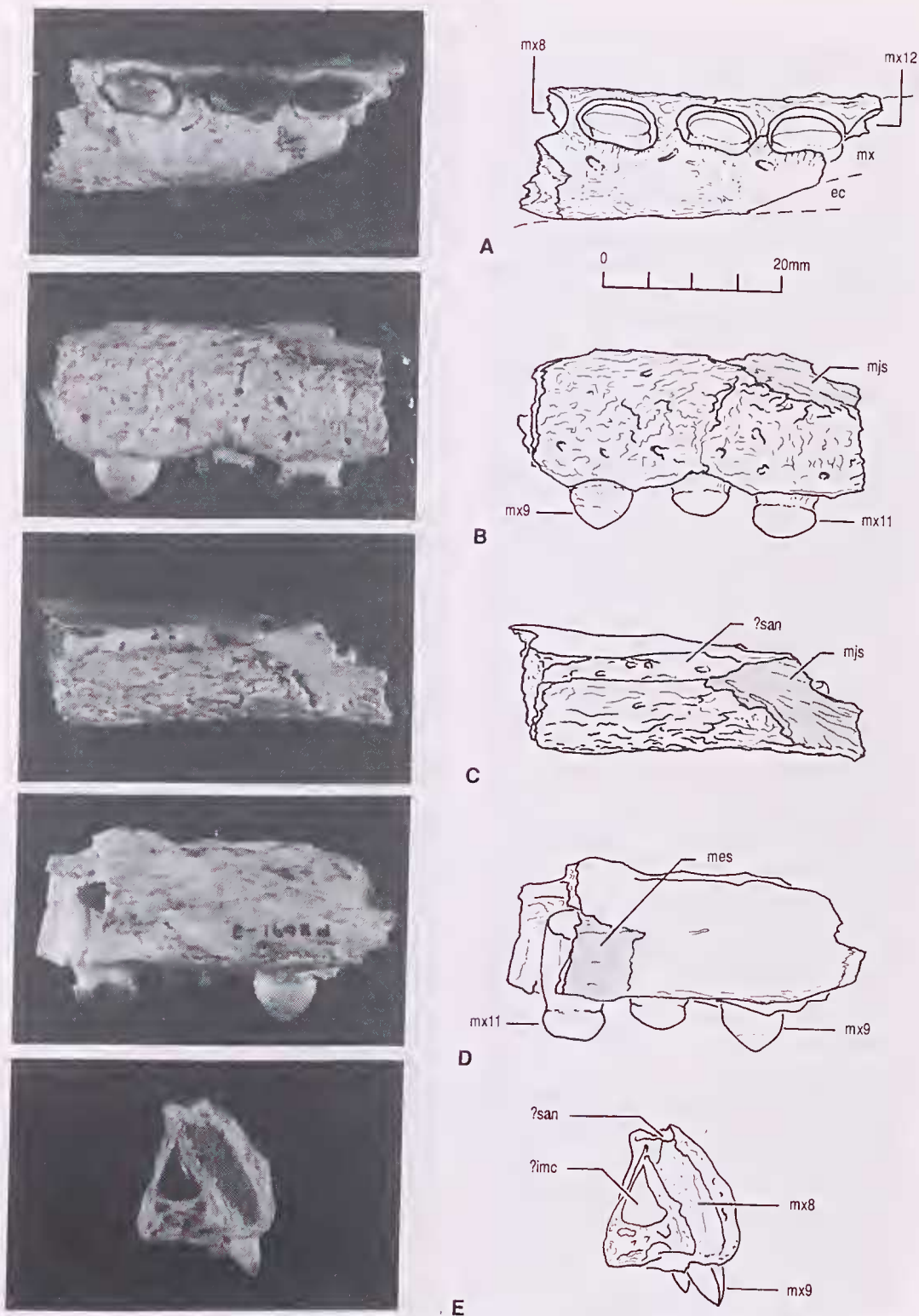


Fig. 5. *Quinkana timara* sp. nov. maxillary fragment NTM P8691-3 in: A, ventral; B, left lateral; C, dorsal; D, medial; and E, posterior views. Sutural surfaces are shown in stipple. Abbreviations: ec, ectopterygoid; imc, intra-maxillary chamber; mes, maxillo-ectopterygoid suture; mjs, maxillo-jugal suture; mx, maxilla; mx8-mx12, maxillary tooth (or its alveolus), numbered from the anterior end.

across the palatal maxillo-premaxillary suture and posteriorly to about the level of the third maxillary tooth, the palate is domed in transverse section. Posteriorly, from the level of the third maxillary tooth to the palatal fenestra, the parasagittal region bulges so that in transverse section, the roof of the palate is markedly peaked at the midline (Fig. 3).

Within the snout, the partition separating the narial passage from the maxillary sinuses is incomplete due to breakage, exposing the supra-alveolar 'niche' and 'lateral chamber' (terminology of Molnar 1981) (Fig. 1D). Molnar's 'narrow chamber between the niche and alveolar part of the maxillary wall' (for which the alternative term 'intramaxillary chamber' is proposed) is possibly exposed at the broken anterior end of the paratype NTMP8691-3 (Fig. 5E). In the holotype, the medial part of the lateral chamber separates the narial passage from the palate in the region delimited by the palatal bulges described above.

The palatines are not preserved with the *Q. timara* holotype, though a small segment of the maxillo-palatine suture is preserved on the medial margin of the pterygoid fossa. The unsutured, preserved portion of the maxillary palate indicates that the anterior palatal processes of the palatines did not project anteriorly far, if at all, beyond the anterior margins of the palatal fenestrae, but their shape cannot be determined.

Although the *Q. timara* holotype right jugal is incomplete posteriorly, it preserves a shallow sub-orbital sulcus that was almost certainly confluent with a lateral concavity such as that preserved on the left maxilla of the holotype. The jugal projects forward beyond the level of the anterior margin of the orbit (Fig. 2B), in the typical Eusuchian fashion. Ventrally, the *Q. timara* jugal has a deeply-sculptured, triangular area adjacent to the transversely-broad maxillo-jugal suture.

Further details are provided by the more complete, isolated jugal NTM P8697-2 (Fig. 7). This specimen represents a larger individual than the holotype, and is shown in Figure 7 in orientations that correspond approximately to the holotype. The ascending process of the postorbital bar, lying in the characteristically Eusuchian sub-dermal position, is relatively more vertical than in crocodiles with relatively flattened skulls, suggesting that the skull table probably projected somewhat over the temporal arcade. The up-turned dorsal margin at the jugal-quadratojugal suture suggests a short anteroposterior dimension for the infratemporal fenestra relative to that

Table 2. Morphometrics of *Quinkana timara* sp. nov. teeth, compared with Pleistocene ziphodont crowns from Croydon, Queensland (after Molnar 1981: Table 2), and *Pristichampsus* spp. examples. *Pristichampsus vorax* data from Langston (1975); UCMPP. *rollinai* data from Langston (1956); Messel (Me) *P. rollinai* data from Berg (1966). Various authors have given measurements with differing accuracy. Few of the *Q. timara* specimens recorded here have a full five millimetre length of serrations preserved, and in these instances the frequency of serrations is recalculated per 5mm. For consistency, the spacing of serrations reported in the literature for *Pristichampsus* species have been recalculated to serrations per 5mm, and rounded off to the nearest whole number. Bracketed figures are estimates; pmx2 and pmx5 = second and fifth premaxillary tooth; mx1 - mx11 = first to eleventh maxillary tooth; d7 = seventh dentary tooth, numbered from the front; ?pmx = not known from where in the tooth row these specimens came.

SPECIMEN	LENGTH	WIDTH	HEIGHT	W/L	SERRATIONS PER 5mm (approx.)
<i>Q. timara</i>					
P895-19					
pmx5	4.7	3.7	-	0.79	-
mx1	5.3	3.7	[12.0]	0.70	40
mx5	[8.3]	[5.0]	-	[0.60]	-
mx6	9.2	3.9	[11.8]	0.42	40
mx7	[6.7]	[3.0]	-	0.45	40
P8691-3					
mx9	8.1	3.6	5.9	0.44	40
mx10	7.1	3.3	3.5	0.46	40
mx11	8.0	3.3	4.2	0.41	40
P894-6					
d7	7.1	3.6	-	0.51	(35)
P862-23					
P87108-24	7.2	3.3	[7.7]	0.46	40
P87111-10	7.2	3.6	[8.3]	0.50	50
P87115-13	7.9	3.3	[8.3]	0.42	35
P87105-43	6.2	2.7	3.5	0.37	40
P862-24	5.9	2.2	3.5	0.37	-
Croydon <i>Quinkana</i> sp.					
QM F9220	16.0	10.3	-	0.64	18-19
QM F9225	11.6	7.2	-	0.62	27
QM F9226	12.9	4.3	-	0.54	-
QM F10141	8.0	4.3	-	0.54	25-27
<i>Pristichampsus vorax</i>					
FMNH PR399					
pmx2	10.1	7.0	-	0.69	30
mx2	8.25	6.0	-	0.73	-
mx4	11	6	-	0.55	-
<i>Pristichampsus rollinai</i>					
UCMP 43921					
?pmx	6.6	5.0	16.4	0.76	27-40
	9.9	5.4	18.4	0.55	32-42
	7.6	4.9	12.5	0.64	35-40
Me 5346					
mx5	8.5	4.9	-	0.58	} 35-45
mx6	8.0	4.5	15	0.56	
Me 5671					
pmx2	4.0	3.1	10	0.78	

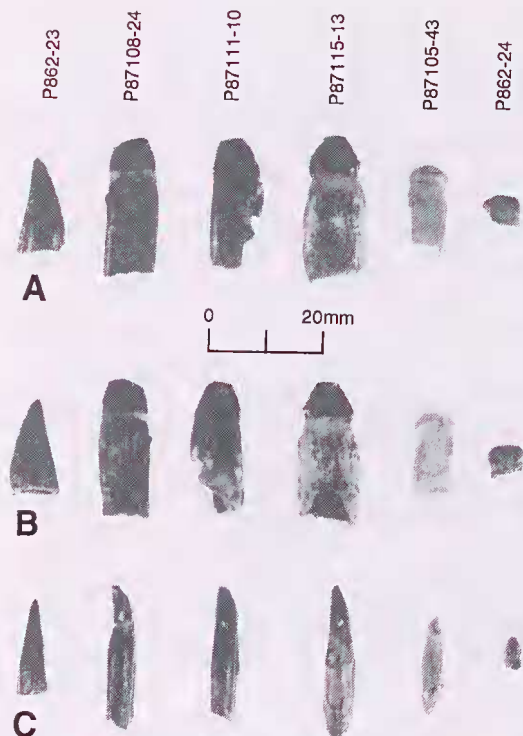


Fig. 6. A selection of isolated ziphodont teeth referred to *Q. timara* sp. nov. in: A, lateral view; B, medial view; and C, anterior or posterior view. Dimensions are given in Table 2.

of the orbit. The extent of the jugal-ectopterygoid suture indicates that there was no posteriorly-directed process of the ectopterygoid along the medial margin of the jugal.

In the *Q. timara* holotype, the laeral and prefrontal are fused to the extent that precise interpretation of their contact is difficult. The interpreted suture appears to pass obliquely between three, just distinguishable, pre-orbital eminences (Fig. 2A).

Dentary fragment NTM P895-16 (Fig. 9), from the mid-region of the dentary ramus, retains four complete and two partial alveoli. The alveoli are of relatively uniform size, laterally compressed, with their long axes slightly inclined to the lateral margin of the dentary, and are medial to small indentations that accommodated the upper dentition.

The other dentary fragment, NTM P894-6 (Fig. 9), includes the symphyseal region. All alveoli are elongated to some degree, with the fourth dentary alveolus markedly so. Dimensions of the *in situ* tooth are given in Table 2. The dorsal surface lateral to the symphysis is narrow and long, while the symphysis extends posteriorly to the level of the sixth dentary tooth. The

splenic is not present, but judging from the sutural trace, terminated anteriorly just short of the symphysis. At about the level of the sixth tooth, the ventrolateral margin of the dentary ramus is expanded into a low crest, increasing in size posteriorly.

Comparative remarks. The comparisons presented here are limited to comparative material at hand and descriptions in the literature. Attention is focussed primarily on ziphodont Eusuchians, namely species of *Pristichampsus* and *Quinkana fortirostrum*, and on selected aspects of other Australian fossil genera and *Crocodylus porosus*.

Snout form. Snout proportions of *Q. timara* are distinctive, and readily distinguish the form from other Australian fossil taxa. Snout proportions of *Q. timara*, *Q. fortirostrum*, *P. vorax* and the Sebecosuchian *S. icaeorhinus* are compared in Table 1 using the method of Molnar (1981) which was devised to accommodate the state of preservation of *Q. fortirostrum*. The *P. rollinatti* specimens described by Kuhn (1938) and Berg (1966) are crushed and distorted, and the illustrations do not lend themselves to calculations of snout proportions. Snout proportions of *P. rollinatti* appear to be comparable to *P. vorax*, as noted by Langston (1975:308-309).

In snout width, *Q. timara* most closely resembles *P. vorax*. The snout is not as narrow as that of *S. icaeorhinus*, while *Q. fortirostrum* is unique amongst the ziphodonts under consideration in having a broad snout. *Quinkana timara*'s snout is somewhat deeper in comparison to that of *P. vorax* and *Q. fortirostrum*, but not as deep as that of *S. icaeorhinus*. Its ratio of rostrum height to length is very similar to that of *P. vorax*, and significantly less than the ratios of *S. icaeorhinus* and *Q. fortirostrum* which are similar to each other.

Features of the premaxillae. The narial aperture of *Q. timara*, like that of *Q. fortirostrum*, is somewhat trapezoidal and wider than it is long, contrasting with the ovoid outline and longer than wide dimensions in *Pristichampsus* species. In both *Quinkana* species, and both *Pristichampsus* species, the dorsal surfaces of the premaxillae are breached within the narial vestibule by the first dentary teeth. In both *Quinkana* species and in *P. vorax*, the narial aperture opens slightly forward and laterally, giving the anterior rostrum a downturned profile in lateral view (Fig. 3). *Quinkana timara* is similar to *Q. fortirostrum* in having no paranasal roofing of the narial vestibule by the premaxilla.

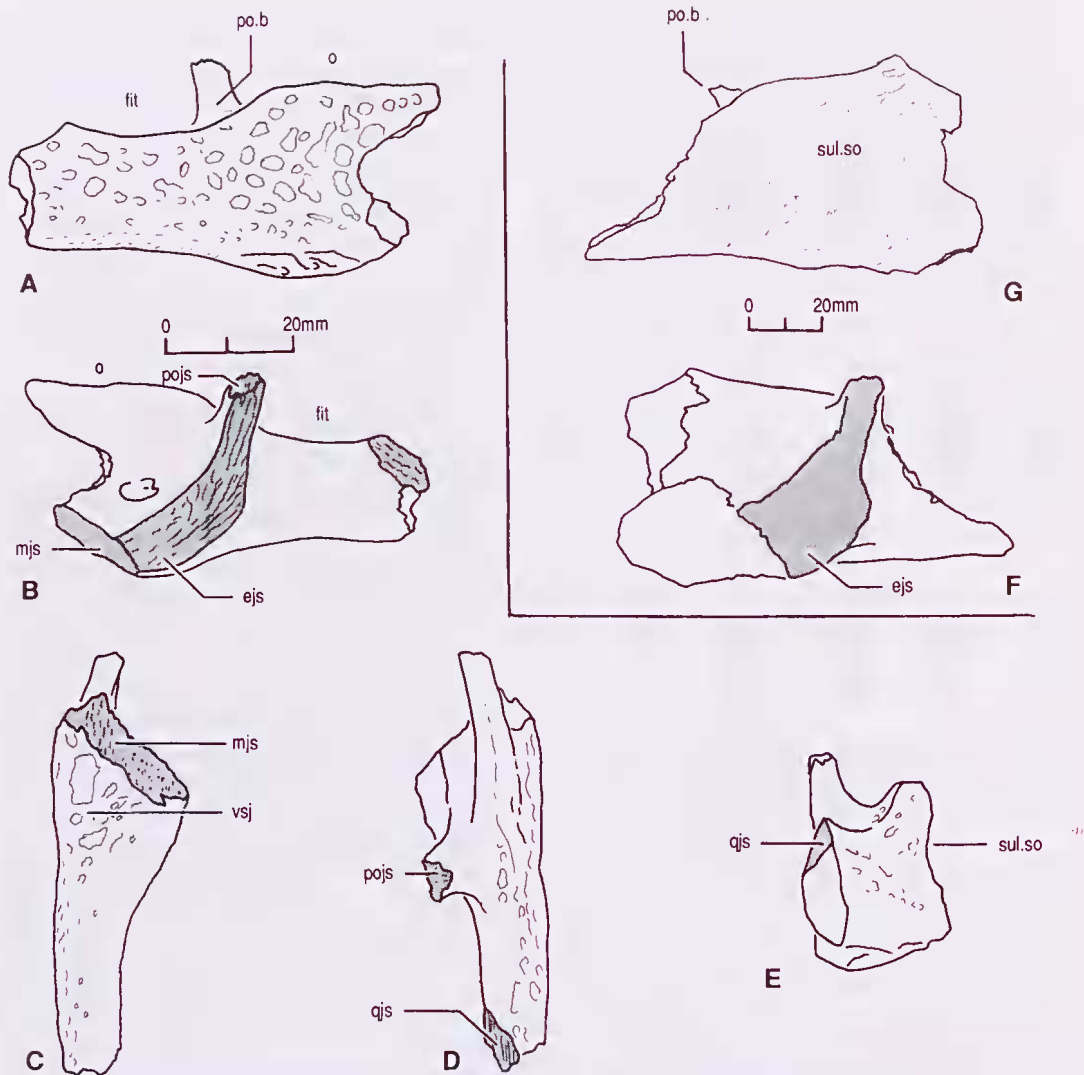


Fig. 7. *Quinkana timara* sp. nov. referred jugal NTM P8697-2 in A, lateral; B, medial; C, ventral; D, dorsal; and E, posterior views, compared with the Pleistocene Chinchilla *Quinkana* sp. jugal QM F1152 in F, medial and G, lateral views (reversed figs after Molnar 1981:figs 11,12). Sutural surfaces are stippled. Abbreviations: ejs, ectopterygoid-jugal suture; fit, infratemporal fenestra; mps, maxillo-jugal suture; po.b., postorbital bar; pojs, postorbital-jugal suture; qjs, quadratejugal-jugal suture; sul.so, suborbital jugal sulcus; vsj, ventral sculptured area of the jugal.

The cardioid or rounded-triangular incisive foramen of *Q. timara* appears to be similarly-shaped, but perhaps proportionally narrower, to that of *Q. fortirostrum*, at least to the extent that a comparison is possible with the incompletely preserved one of the *Q. fortirostrum* holotype. The incisive foramen (=premaxillary foramen of Langston 1975) of *P. vorax* is oval, centred more posteriorly within the narial aperture (Fig. 3), and as noted by Langston (1975:300) "seems to be exceptionally large for a narrow-snouted crocodylian". That of *P. rollinatti* is depicted in a

schematic illustration by Berg (1966: Abb.6) as being small, but of uncertain outline.

Quinkana timara has a subdued rim bounding the external nares about their posterior margin. In *Q. fortirostrum* the homologous structure shows an exaggerated development that is probably indicative of an aged individual. Langston (1975:300) notes that in *P. vorax* "the narial rims are not raised above the level of the adjacent skull bones", though his illustrations of FMNH PR399 suggests a close structural similarity to *Q. timara*, in which a subdued rim is present.

Dentition. *Quinkana timara* had at least 12 maxillary teeth. As restored in Figure 3B, the *Q. timara* maxilla has ample room for a thirteenth maxillary alveolus. The *Q. fortirostrum* holotype has 12 alveoli preserved on the left maxilla, which is also incomplete posteriorly. Molnar (1977) considered there to be insufficient room for additional teeth posterior to the twelfth because of the marked narrowing of the maxilla. However, in this region the maxilla was lapped by the ectopterygoid, as evidenced by the trace of the maxillo-ectopterygoid suture. In many Eusuchians, for example *P. vorax* (Fig. 3A), the ectopterygoid, separated from the medial walls of the most posterior alveoli by only a thin lamina of maxillary bone, compensates for the narrowing of the maxilla. Thus, *Q. fortirostrum* may have had more than twelve maxillary teeth. By comparison, *P. rollinatti* had 13 maxillary teeth (Berg 1966), while *P. vorax* had 16 or 17 (Langston 1975). Both *Quinkana* species and *Pristichampsus vorax* have alveoli for five pre-

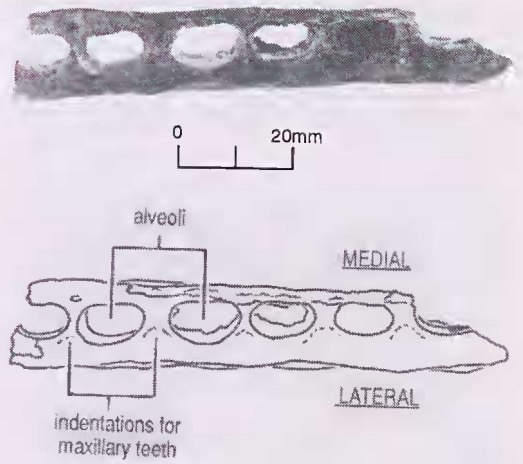


Fig. 8. *Quinkana timara* sp. nov. dentary fragment, NTM P895-16, in occlusal view showing equidimensional, evenly spaced alveoli with their long axes inclined slightly to the margins of the dentary, and evidence that the maxillary teeth closed lateral to the dentary teeth.



Fig. 9. *Quinkana timara* sp. nov. paratype dentary fragment NTMP894-6 in A, dorsal; B, medial and C, lateral views. Abbreviations: dc, dentary crest; ds, dentary symphysis; dss, dentary-splenial suture; d1 - d7, dentary tooth or its alveolus, numbered from the anteriorend.

maxillary teeth, and *P. rollinatti* is restored as having five (Berg 1966: Abb. 6a).

The apparent variation in tooth size, reflected in alveolar dimensions, along the tooth row in *Q. timara* appears to be somewhat greater than in *Q. fortirostrum*, and more closely resembles variation in *P. vorax* and *P. rollinatti*. *Quinkana fortirostrum* shows the least development of festooning, with *P. vorax* and *Q. timara* showing relatively more (Fig. 3). The snout of *P. rollinatti* is described by Berg (1966:69) as being vertically festooned: "Der untere dieser cranialen Schnautzenwände ist 'festoniert'", but to what degree is not expressed. Kuhn (1938: 322) indicates that it is reasonably well developed "...die Festonierung (ist) noch ziemlich stark aus-gesprägt..".

In both *Quinkana* species, the maxillary alveoli (and in the case of *Q. timara*, the *in situ* teeth) typically have their long (anteroposterior) axes inclined to the lateral margin of the maxilla. However, this condition may not be obvious in some views because of parallax effects. For example, it is most obvious in *Q. fortirostrum* from a slightly ventrolateral perspective (Fig. 10) rather than a strictly ventral aspect (compare with Molnar 1981: fig. 3). Figures 1B and 5A most clearly illustrate the condition in *Q. timara*. Langston (1975) does not comment on the orientation of the maxillary alveoli of *P. vorax*. Many of the alveoli of *P. vorax* appear quite round (Langston 1975: fig. 1B), but many are also drawn with somewhat vague outlines, so the orientation of their principal axes cannot be gauged. In a restored, schematic view, Berg (1966: Abb.6) shows the alveoli of *P. rollinatti* as markedly oval in outline, with their long axes parallel to the snout margins. The second maxillary tooth of *P. vorax* (FMNH PR399) resembles the first maxillary tooth of the *Q. timara* holotype in having a distinct posterior curvature. Berg (1966:69) observed that the teeth of *P. rollinatti* (evidently Me 5346) are gently curved and compressed: "Die Kronen der Zähne der Messelfunde entsprechen in der leicht gebogenen ..., abgeflachten Form..".

Langston (1975) gives principal basal diameters of three *in situ* teeth in FMNH PR399 (*P. vorax*), while Berg (1966) provides comparable detail on some *in situ* teeth of *P. rollinatti*. The teeth of both taxa are comparable to those of *Q. timara* and Croydon *Quinkana* sp. (Table 2). AMF57844, the sole specimen of *Q. fortirostrum*, is edentulous, but I agree with Molnar's inference (1977, 1981), based on alveolar morphol-

ogy, that this species was a ziphodont *sensu stricto*. *Quinkana timara* is represented by sufficient *in situ* teeth to demonstrate a general pattern of the teeth becoming proportionally more compressed, and lower, along the tooth row posteriorly.

Quinkana timara teeth average seven to ten serrations per millimetre on the carinac, which is approximately twice as many as recorded by Molnar (1981: table 2) for Pleistocene *Quinkana* sp. teeth from Croydon, Queensland (Table 2). Langston (1975: 308) records six serrations per millimetre on a *P. vorax* tooth. Kuhn (1938: 322) describes the teeth of *P. rollinatti* (= *Weigeltisuchus geiseltalensis*) as being dinosaur-like, (?ribbed), compressed and serrated: "Die an Saurischier erinnernden Zähne sind meist hippenförmig (= ?rippenformig), komprimiert und gesägt". Langston (1956: table 1) found the frequency of serrations on individual *P. rollinatti* teeth from Argenton, France, to be variable, with three teeth exhibiting a range of 5.5 to 8.4 serrations per millimetre. Berg (1966: 72) records seven to nine serrations per millimetre in Messel (Germany) specimens of *P. rollinatti* (Table 2).

Shape of the palate. *Quinkana timara*, *Q. fortirostrum* and *P. vorax* all have, in transverse sections (Fig.3), a domed anterior palate, and a peaked profile between the parasagittal bulges posteriorly. The alveoli are housed in alveolar processes which project ventrally below the level of the palate. The condition in *P. rollinatti* cannot be ascertained from the available literature.

Internal structure of the rostrum, extent of the palatine, and pterygoid fossa morphology. These three aspects of morphology are treated together

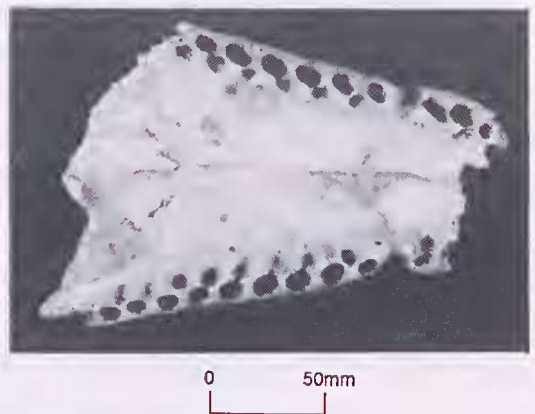


Fig. 10. A slightly right-lateral, ventral view of the *Quinkana fortirostrum* holotype AMF57844, that best shows the inclination of the alveoli to the right (upper in photograph) margin of the snout.

here because they may be part of a single complex. The sutural relationship of the palatines to the maxillae are of some interest as possible systematic indicators. Willis *et al.* (1990), as part of a preliminary assessment of the systematic position of the mid-Tertiary crocodylian *Baru darrowi*, hypothesised that the lack of, or marked reduction of, the anterior palatine process might represent a shared derived character state of a natural group of crocodylids containing extinct Australian genera, including *Quinkana*. Additional cleaning of the *B. darrowi* holotype has revealed that the the maxillo-palatine sutures depicted in Willis *et al.* (1990: fig. 1) represent a fracture, rather than sutures. The morphology of the maxillo-palatine sutures of *Q. fortirostrum* and *B. darrowi* are both illustrated in Figure 11, and contrasted with the living estuarine crocodile, *Crocodylus porosus*. A detailed description of this region in *Q. fortirostrum* is provided by Molnar (1981), and only selected aspects are repeated here.

The internal structure of the *Q. timara* holotype corresponds closely with that described by Molnar (1981) for the Pleistocene Texas Caves *Quinkana* sp. QM F7898, and is consistent with what can be seen within the snout of the *Q. fortirostrum* holotype. Both *Q. timara* and *Q. fortirostrum* have the "lateral chamber" of Molnar (1981), which is also present in other crocodylians (e.g. *Crocodylus* spp., Molnar 1981, and Fig. 11). In *Crocodylus porosus* the lateral chambers do not extend between the palate and narial passage, but do in juvenile *Baru*, where they become reduced or disappear in growth. Their more extensive development in *Quinkana* and *Baru* is almost certainly related to the depth of the skull.

In palatal view, the palatal fenestrae of *C. porosus* extend anteriorly to the level of the ninth maxillary tooth. The combined anterior palatine processes appears as a large, lobate structure projecting forward to the level of the seventh maxillary tooth. Anteriorly, the palatine bone is flat, flaring laterally and lapping the maxilla so that it forms part of the anteromedial margin of the palatal fenestra. The anterior edge of the palatal fenestra is sharp because the pterygoid fossa continues forward above the palate, terminating at a medial projection of the lateral maxillary wall (Fig. 11).

In *Q. fortirostrum*, both the palatal fenestrae and the anterior extremities of the palatines extend to the level of the seventh maxillary tooth in palatal view. The maxillo-palatine suture follows

a posteriorly-open, broad V-shaped trace between the anteromedial margins of the palatal fenestrae. The indications are that *Q. timara* also had a short palatine process, with the anterior margin of the palatal fenestra aligned with the eighth maxillary tooth. In *Q. fortirostrum* (and *Q. timara*), the pterygoid fossa does not continue forward above the bony palate, but terminates at "a high, posteriorly concave partition dorsally bound(ing) the anterior margin of the palatal fenestra" (Molnar 1981:807). Molnar conceptualised the wall as representing a medially complete version of the projection of the lateral maxillary wall in *Crocodylus*, as described above. The *Q. fortirostrum* holotype (AM F57844) is sufficiently complete to show that the palatines participate in this wall medially, so the condition, relative to *Crocodylus*, might more realistically be thought of as a dorsal folding (along a curved axis) of part of the palatal and maxillary palate.

The holotype *Baru darrowi* specimen NTM P8695-8, a mature adult, is similar to *Q. fortirostrum* in having the pterygoid fossa walled anteriorly and part of the palate folded dorsally, but the maxillo-palatine suture and lateral chamber morphology are not identical (Fig 11). The anterior palatine process is quite large and lobate, terminating anteriorly slightly forward of the palatal fenestrae, and is reminiscent of *Asiatosuchus* and *Osteolaemus*. The lateral chamber of *Baru* extends posteriorly alongside the narial passage to well behind the anterior margin of the palatal fenestra, and appears to open through a small foramen into the medial wall of the pterygoid fossa. A post-hatchling *Baru* specimen (NTM P87105-6) appears to have an unfolded palate (Fig. 11), with a lateral chamber terminating at, and opening through, a proportionally large foramen in the anterior wall of the pterygoid fossa. A slightly larger individual (NTM P87103-8) has similar lateral chamber morphology, but shows signs of incipient palatal folding (Fig. 11).

In the skull of *Crocodylus porosus* sectioned for illustration in Figure 11, the lateral chamber is confluent with the narial passage, though the opening of the lateral chamber lies outside the direct line of the narial passage as extrapolated anteriorly from the lateral margins of the vomers. Vomer morphology of *Baru* is unknown. The "two thin, nearly vertical flanges, which together form a narrow trough along the floor of the snout cavity" of *Q. fortirostrum* (Molnar 1981: 807)

are in sutural contact with the maxilla, and represent the anterior parts of the vomers (Fig. 11), and are not part of the maxilla as described by Molnar (1981). The anterior extent of the vomers cannot be determined in the *Q. fortirostrum* holotype because they are still partly embedded in matrix, while the relationship of the narial passage to the lateral chambers of *Q. fortirostrum* cannot be determined because of the lack of preservation of the vomers posteriorly.

Iordansky (1973: fig. 14) labels the opening of the lateral chamber in *Crocodylus* sp. as "an accessory air cavity of the narial passage", but it would be interesting to dissect a fresh specimen to determine whether the narial passage is isolated from the lateral chamber by soft tissue, and whether the lateral chamber is connected to the pterygoid fossa, rather than the narial passage, as suggested by the morphology of *Baru*. Excluding the lateral chamber, ramifications of the narial passage in the form of accessory chambers are present in *Crocodylus*, but absent in *Quinkana* and *Baru* (Fig. 11).

The palatal view of *P. vorax* (Fig. 3A; after Langston 1975: fig. 1b) shows the anterior palatine processes projecting slightly beyond the anterior edge of the palatal fenestrae, but the morphology of its pterygoid fossae and internal structure are undescribed. Berg (1966) portrays a palatine process projecting beyond the palatine fenestrae in *P. rollinatti*, but his use of dashed lines suggests some uncertainty in the interpretation. Pterygoid fossa morphology and internal structure is not described for *P. rollinatti*.

In Eusuchians, the combined palatines typically project anteriorly as a lobate structure on the palate, often beyond the anterior margins of the palatal fenestrae. Amongst living Eusuchians, *Osteolaemus tetraspis* Cope and *Tomistoma schlegelii* (Muller) have the palatines terminating anteriorly at about the level of the anterior margin of the palatal fenestrae. However, these taxa differ in that the anterior palatinal processes of *Osteolaemus*, though lying entirely between the palatal fenestrae, appears lobate in palatal view, while the maxillo-palatine sutures of *Tomistoma* basically taper forward, meeting as a posteriorly-open, broad V, though in this species the maxillo-palatine relationship is complicated by palatal exposure of the vomers (=pre-vomers of Mook 1921; see Mook 1921: 145, fig. 2 and Iordansky 1973: fig 3 for variability in *T. schlegelii*). However, palatal features in longirostrine forms may be determined by skull conformation so that comparison of maxillo-

palatine sutures between brevirostrine and longirostrine forms may be problematic.

Willis *et al.* (1990) considered the possibility that the palatal trace of the maxillo-palatine sutures might simply relate to the relative size of the palatal fenestrae. It is well known that long, narrow-snouted crocodylians tend to have small palatal fenestrae, while short, broad-snouted forms typically have larger ones (e.g. Iordansky 1973). Willis *et al.* (1990) observed that while *Osteolaemus* has large palatal fenestrae, it also has large, lobate anterior palatine processes similar to those present in alligators and *Crocodylus*, though not projecting beyond the palatal fenestra, and that therefore the two structures seem to be independent character states.

The maxillo-palatine suture of *Baru darrowi* was interpreted by Willis *et al.* (1990) to resemble *Quinkana fortirostrum* and the North American Eocene species *Brachyuranochampsia eversolei* Zangerl, 1944. With further preparation (Fig. 11), *Baru* appears to more closely resemble *Asiatosuchus germanicus* (Berg 1966) and *Osteolaemus*; i.e. with the palatines projecting to about the level of the anterior margins of the palatal fenestrae (as remarked upon by Berg 1966: 55), but having a lobate structure. Willis and Molnar (1991) depict the maxillo-palatine suture of *Australosuchus clarkae* resembling that of *Quinkana fortirostrum*, but it is not clear how the shape was determined from the described material.

Jugal morphology. The jugal of *Q. timara* is similar to Queensland *Quinkana* sp. material in having a ventral sculptured area. Molnar (1981: 815) likens the ventral sculptured area in his *Quinkana* sp. material to the condition in *Alligator mississippiensis* (Daudin), but gives no indication of its shape. In *Q. timara* specimens, the ventral maxillo-jugal suture is quite broad. No ventral sculptured area such as that present in *Q. timara* is present in the other two named fossil taxa from Bullock Creek, *B. darrowi* and *H. camfieldensis*. The *B. darrowi* and *H. camfieldensis* holotypes have short, less transversely oriented jugal-maxillo contacts in ventral view (Willis *et al.* 1990, Megirian *et al.* 1991). The jugal of *H. camfieldensis* is gracile alongside the infratemporal fenestra and has a robust postorbital bar. The sub-orbital sulcus in *Q. timara* is more weakly developed than in *B. darrowi*, and there is no prominent lateral jugal ridge as described in Willis *et al.* (1990: fig 1A). As mentioned in the description of *Q. timara*, the paratype jugal is from a larger individual than

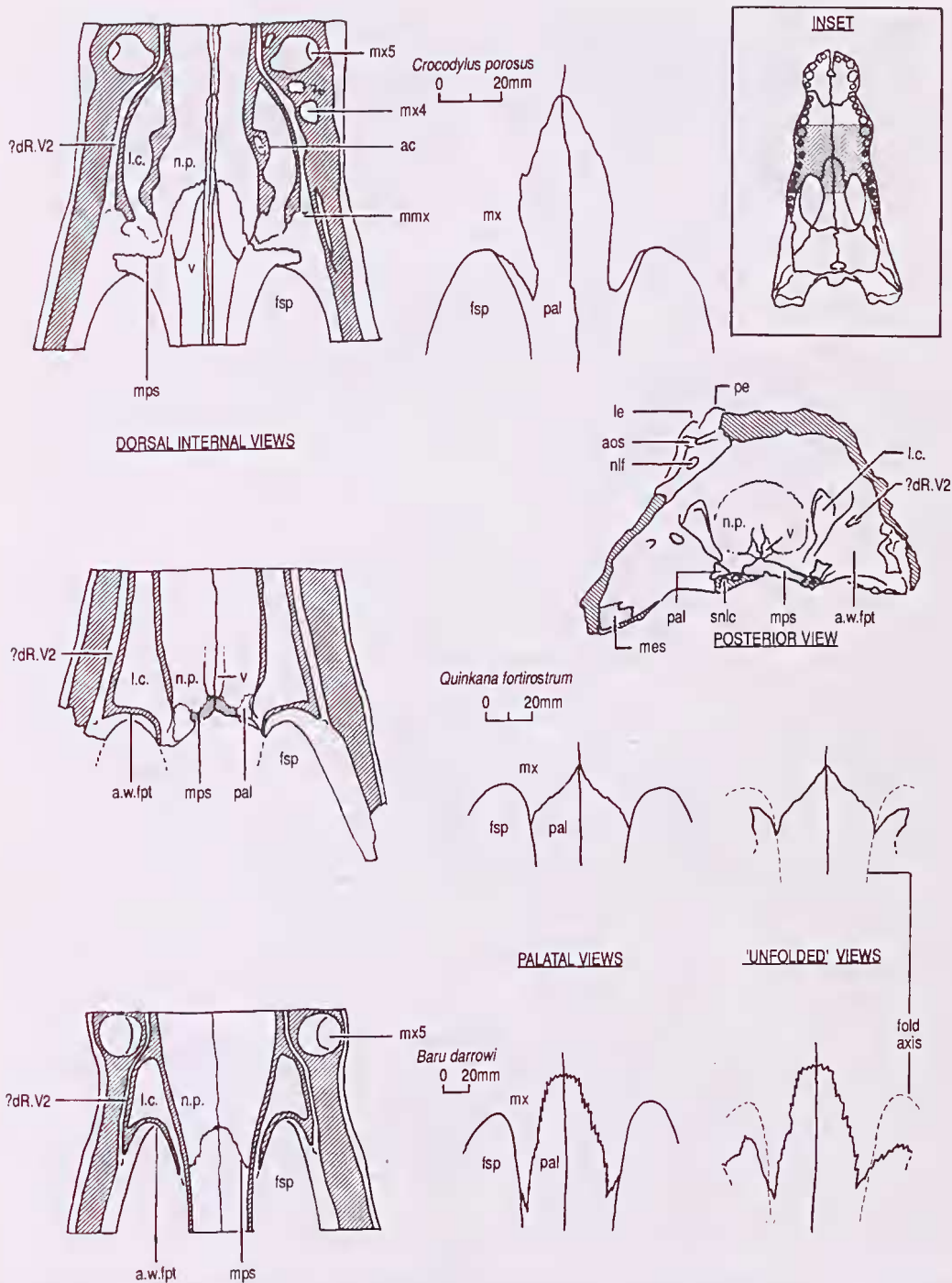


Fig. 11. A comparison of palatine-maxillary relationships and internal structure of the mid-palatine region of the rostrum in: A, *Crocodylus porosus*; B, *Quinkana fortirostrum* (schematic); and C, *Baru darrowi* (schematic). INSET: a crocodylid skull in ventral view showing the region of the skull being compared. Vomer morphology is unknown for *Baru*, while the palatal maxillo-palatine sutural contacts of *Baru* and *Quinkana* are restorations prepared from plasticine impressions. Sutural surfaces are shown in stipple, and sectioned or broken surfaces are hatchured. Abbreviations: ac, accessory chamber of the narial passage; aos, ante-orbital shelf; a.w.fpt, anterior wall of the pterygoid fossa; ?dR.V₂, ?duct for Ramus maxillaris nervi trigemini; fsp, palatal fenestra, l.c., lateral chamber; le, lacrimal eminence; mes, maxillo-ectopterygoid suture; mps, maxillo-palatine suture; mx, maxilla; mx5, fifth maxillary alveolus; nlf, nasolacrimal foramen; n.p., narial passage; pal, palatine; pe, preorbital eminence; snlc, sub-narial portion of the lateral chamber; v, vomer.

the holotype, and is more robust, and probably proportionally deeper. However, the two jugals seem to fall within the range of allometric variability expressed in NTM *E. porosus* samples. Langston (1975) records two suborbital sulci in

P. vorax, but his illustrations convey no specific detail about ventral jugal morphology.

Molnar (1977, 1981) was mistaken in describing the jugal of *Q. fortirostrum* as not projecting beyond the orbit. The maxillo-jugal suture is

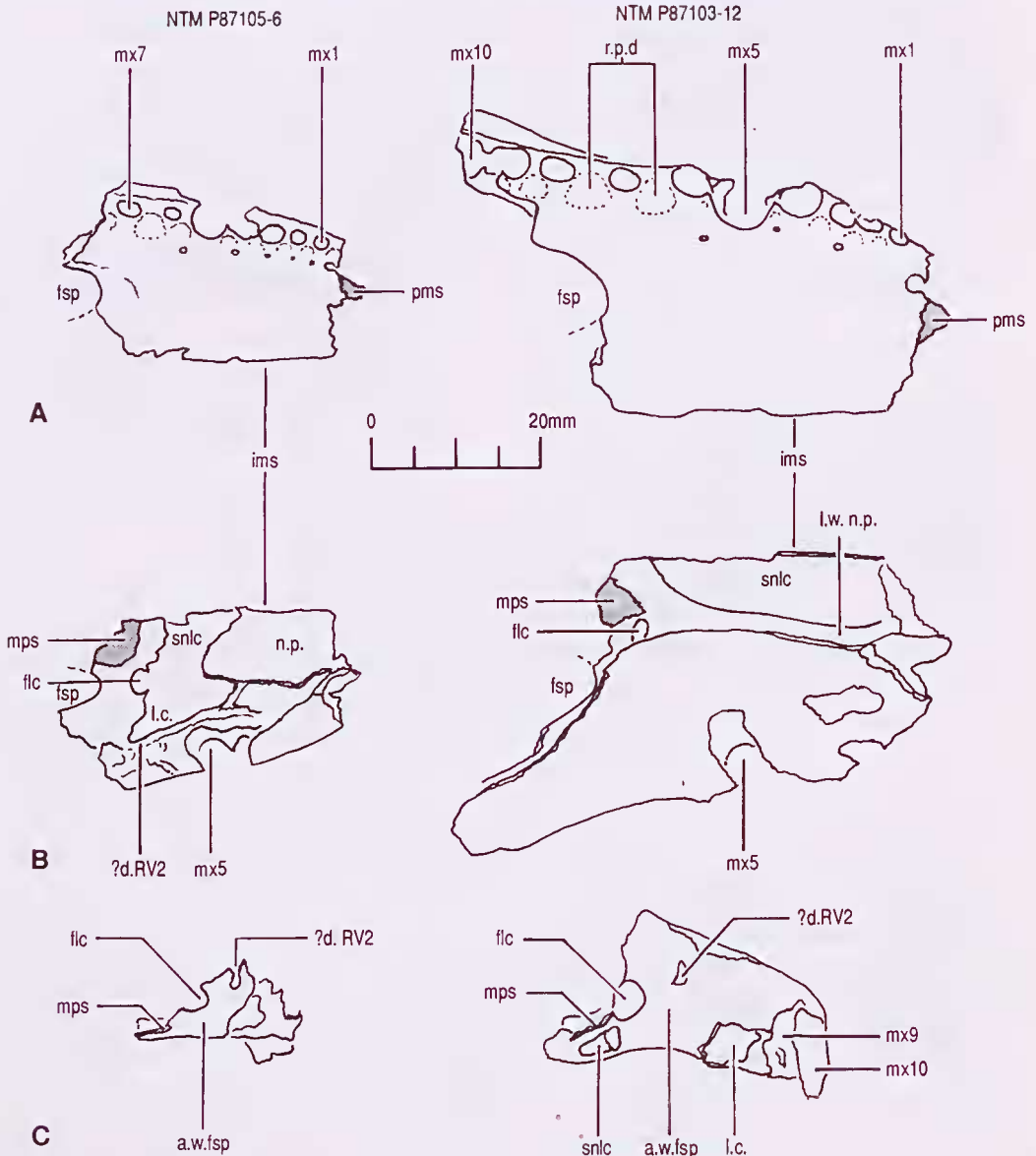


Fig. 12. Two maxillae of juvenile *Baru darrowi*. A, palatal views showing the distinctive features of the taxon, for comparison with Willis *et al.* (1990: fig. 1); B, dorsal views; C, posterior views. In the smaller individual, the maxillo-palatine suture lies parallel to the palatal plane, and the lateral chamber does not extend ventral to it. In the slightly larger individual, the maxillo-palatine suture is inclined to the palate in posterior view, and the lateral chamber is visible below the suture. The condition in the larger specimen is interpreted to be structurally intermediate to the condition in a mature individual (Fig. 11), where the homologous part of the maxillo-palatine suture is not visible in dorsal view, and the lateral chamber is lateral to the narial passage. Abbreviations: a.w.fsp, anterior wall of the pterygoid fossa; ?d.RV2, duct for Ramus maxillaris nervi trigemini; flc, foramen of the lateral chamber; fsp, palatal fenestra; ims, intramaxillary suture; i.c., lateral chamber; l.w.n.p., lateral wall of the narial passage; mps, maxillo-palatine suture; mx1 - mx10, maxillary alveoli numbered from the front; n.p., narial passage; pms, premaxillo-maxillary suture; r.p.d., reception (occlusal) pit for a dentary tooth; snlc, sub-narial extension of the lateral chamber.

clearly visible in the Texas Caves cranium, both externally and internally (Fig. 3C), and its anterior projection beyond the orbit is typically Eusuchian, and resembles *Q. timara* and *P. vorax* in its extent. Although the jugal posterior to the anterior orbit margin is not known for *Q. fortirostrum*, it was clearly deep dorsoventrally, and the presence of a probably shallow sub-orbital sulcus is indicated by the portion of the jugal preserved.

One possibly significant difference in *Q. timara* when compared to the Pliocene Chinchilla *Quinkana* sp. jugal is the relatively smaller extent of jugal-ectopterygoid sutural contact (compare Fig. 8B and F). In *P. vorax*, the posterior ramus of the jugal, where it bounds the infratemporal fenestra, is deflected ventrally (Fig. 3A), contrasting with the unflexed arrangement in *Q. timara*.

Structure of the preorbital, post-premaxillary surface of the rostrum. *Quinkana fortirostrum* exhibits dramatic development of excrescences and ridges on the dorsal surface of the rostrum (Molnar 1977, 1981), including the expression of the narial rim on the premaxilla described above. The lacrimal bears two distinct knobs and the prefrontal bears a single knob, the maxilla has a prominent ridge or crest at the transition from the dorsal to the lateral surfaces of the snout, a crest lies over the first maxillary tooth, and the nasals are greatly thickened. Homologous structures can be distinguished in *Q. timara* on the lacrimal, prefrontal and maxilla, though their expression is much more subtle. The nasals cannot be compared because they are not known for *Q. timara*. The exaggerated development of these structures in *Q. fortirostrum* may be related to age.

Another structure shared by the two species of *Quinkana* is a distinct antorbital shelf, of unknown function, lying directly above the nasolacrimal duct, and laterally adjacent to the base of the prefrontal eminence. The shelf in *Q. timara* is proportionally larger than that of *Q. fortirostrum*. The two species of *Quinkana* are structurally identical about the orbit, only differing in the degree of expression of lacrimal and prefrontal excrescences, and the antorbital shelf.

Apart from a preorbital maxillary crest, none of the structures present in *Quinkana* are specifically mentioned by Langston (1975) for *P. vorax*. I can recognise no specific reference to the development of structures on the dorsal surface of *P. rollinatti* in Berg (1966) or Kuhn (1938).

Discussion and concluding remarks. *Quinkana fortirostrum* and *Quinkana timara* sp. nov. share a distinctive ziphodont dentition and pattern of development of excrescences on the dorsal surface of the rostrum, justifying the assignment of the new Bullock Creek form to the genus *Quinkana*, and distinguishing these species from other described Australian fossil taxa. The literature on *Pristichampsus* species makes no mention of such characters, nor are they apparent in illustrations.

In terms of trophic specialisation and skull conformation, *Quinkana timara* is most similar to species of *Pristichampsus*, sharing a suite of characters that have been interpreted as advantageous for a terrestrial mode of life. *Quinkana fortirostrum* differs notably from these ziphodont ecomorphs in having a relatively broader snout (Molnar 1977, 1981). Whether these features support an interpretation of close relationship, or are yet another example of convergent evolution in crocodylomorphs, is unclear.

When dealing with fragmentary material from a number of quarries known to contain several poorly-understood species, there is always the possibility that individual specimens are misidentified. At the time *B. darrowi* was described, there was little idea of the diversity of crocodylian taxa at the type locality (Bullock Creek), or in other northern Australian Miocene limestone deposits (e.g. Willis 1992). I now suspect that part of a cranial table (NTM P87103-11) designated a paratype of *B. darrowi* in Willis *et al.* (1990), and used in its restoration, represents *Q. timara*. The fragment is too small to represent the *Q. timara* holotype individual. Willis *et al.* (1990: 535) noted that features of the incompletely preserved NTM P87103-11 quadrate "...are more reminiscent of *Pristichampsus* than *Crocodylus*". I reserve a re-evaluation of NTM P87103-11 until it is possible to differentiate the skull table of *Q. timara* sp. nov. from that of *B. darrowi* and other possible *Baru* species (Archer *et al.* 1991: 69, Willis 1992).

The systematic position of *Quinkana* within the Eusuchia cannot at this time be satisfactorily resolved using cladistic methods. Benton and Clark (1988) presented a phylogenetic analysis of the Archosauria, establishing the Eusuchia as a monophyletic group of crocodylians. More recent work has focussed on more firmly establishing outgroups to the Eusuchia as a step towards more satisfactorily resolving relationships within the group (Norell and Clark 1990, Clark and

Norell 1992). Clark and Norell (1992) diagnose the Eusuchia by the following synapomorphies: 1, posterior intrapterygoid position of the choana; 2, procoelous trunk vertebrae; 3, procoelous cervical vertebrae; 4, strongly convex condyles on the biconvex first caudal vertebra and 5, dorsal osteoderms lacking a smooth, raised area on their anterior dorsal surface. The Crocodylia are defined as a crown group comprising the living Eusuchians and the descendents of their closest common ancestor, though no entirely satisfactory diagnosis has been put forward. Norell (1989) provides a phylogenetic analysis of the living Crocodylia, in which he recognises three natural groups, referred to informally as 'crocodylids', 'alligatorids' and 'gavialids', which are comparable to the concept of the Alligatorinae, Crocodylinae and Gavialidae *sensu* Kälin (1955), for example. However, these studies do not provide a suitable basis for evaluating the position of *Quinkana* within the Eusuchia, or the relationship of Australian fossil genera to each other. At the higher taxonomic level, the scheme is heavily dependent on post-cranial characters, which are not known for *Quinkana*, while more generally, insufficient cranial characters of systematic significance are known or adequately documented for the Eusuchia. Additional limitations result from incomplete representation of the taxa of interest, precluding direct comparison. Thus, at this stage it is only possible to consider whether the form has 'enough' of the 'key' characters that distinguish some of the recognised groupings.

Molnar (1981) provided a character state assessment of *Quinkana fortirostrum* using a method based on the system of Hecht (1976) and Hecht and Edwards (1976). He established polarities of 18 cranial characters (not all of them considered by him to be useful in determining relationship) largely by 'commonality of the state' amongst 34 crocodylian genera, and was successful in resolving *Q. fortirostrum* as a ziphodont crocodylid. Molnar (1977) initially suggested *Quinkana fortirostrum* might also belong to the Pristichampsinae Kuhn, 1968, but later designated it sub-family *incertae sedis* (Molnar 1981: table 4).

Willis *et al.* (1990) recognised in *Baru*, *Pallimnarchus* and *Quinkana* a suite of characters that distinguished these forms from extant crocodylids (e.g. *Crocodylus*), and noted that they shared similarities with certain Paleogene taxa from North America and Europe. Willis and Molnar (1991) recognise similar features in

Australosuchus. Molnar (1981) suggested that a reduced anterior process of the palatine might be a derived condition in Eusuchians. Willis *et al.* (1990) went so far as to suggest that this character state might be a synapomorphy of a clade within the Crocodylidae. The more detailed comparison presented here of the palatal region of *Quinkana fortirostrum*, *Crocodylus porosus* and *Baru darrowi* indicates that additional studies, incorporating a greater range of taxa, are needed. While there are certainly some similarities between *Baru* and *Quinkana*, it is not clear that their respective palatal morphologies are homologous.

Detailed comparative studies are also needed to determine whether *Quinkana*, *Baru*, *Pallimnarchus* and *Australosuchus* have shared, derived character states diagnosing a clade (Willis *et al.* 1990). The structural similarities between *Quinkana timara* and *Pristichampsus* species suggest that a pristichampsine designation for *Quinkana* cannot be ruled out.

Etymology. In the mythology of the Yalanji people of Cape York, as retold by Trezise and Roughsey (1982), the Timara are thin Quinkins (spirits). The allusion is to the narrower snout of *Q. timara* relative to *Q. fortirostrum*.

NOTE ADDED IN PROOF

In the interval between the preparation of this manuscript and its appearance in print, several developments have occurred. Two additional Australian fossil taxa have been described, namely *Kambara murgonensis* Willis, Molnar and Scanlon, 1993, and *Trilophosuchus rackhami* Willis, 1993a. Additional crocodylian research in progress during the period 1990 to 1993 is reviewed in Willis (1993b).

Willis *et al.* (1993a) expanded the Willis *et al.* (1990) concept of a monophyletic radiation of extinct Australian crocodiles (which includes *Quinkana*) to encompass the New Caledonian form, *Mekosuchus inexpectatus* Balouet and Buffetaut, and formally designated the clade the Mekosuchinae. Within this concept of the Mekosuchinae, *Kambara*, a morphologically generalised crocodile, is the most plesiomorphic representative. *Trilophosuchus* is not mentioned in Willis *et al.* (1993), but is portrayed in a dendrogram in Willis (1993a) as being the plesiomorphic sister taxon to the genera included in the Mekosuchinae. *Trilophosuchus*

has not lost the anterior palatine process, a character nominated as a synapomorphy of mekosuchine genera. The origins of the radiation remain obscure.

In its functional morphology, *Trilophosuchus* is similar in some respects to the living *Osteolaemus* and *Palaeosuchus*, but is perhaps more similar to extinct forms such as *Notosuchus*, *Araripesuchus*, *Libycosuchus* and *Notosuchus* (Willis 1993a). Willis concludes that the Australian form may have been terrestrial in its habits, but occupying a niche distinct from that possibly favoured by the *Pristichampsus*-like ziphodont crocodylians.

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